# MONOGRAPH OF LOPHOPTERYS (MALPIGHIACEAE) 

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#### Abstract

Lophopterys Adr. Juss. is a South American genus of Malpighiaceae comprising seven species, two of which are described here as new (L. floribunda W. R. Anderson \& C. C. Davis and L. occidentalis W. R. Anderson \& C. C. Davis). The taxonomic history, morphology, circumscription, and systematic position of the genus are discussed, with the conclusion that while the genus is coherent and easily recognized, its relationships in the family are still somewhat obscure. The taxonomy is revised with descriptions, keys, and notes on phenology, habitat, and distribution, and all specimens studied are cited. Illustrations include a distribution map, SEMs of pollen from two species, and drawings of six species.


## INTRODUCTION

Lophopterys is a small South American genus of Malpighiaceae, which as recently as 1951 seemed to be wholly restricted to the Guianas. We now know that the genus is widespread (Fig. 1), with collections known not only from the Guianas, but also from Amazonian Venezuela, Peru, Bolivia, and Brazil, and from extra-Amazonian southeastern Brazil. Our purpose in this paper is to review the history, circumscription, and possible relationships of the genus, and to offer a taxonomic revision of the known species.

## TAXONOMIC HISTORY

The genus Lophopterys was described by Adrien de Jussieu (1838) on the basis of a fruiting collection by Poiteau from somewhere in French Guiana, which Jussieu called Lophopterys splendens. The generic name means "crest-wing" and refers to the fact that each mericarp in the type species bears only a dorsal crest (see Fig. 7 g ). The specific epithet, meaning shining or brilliant, undoubtedly referred to the persistently metallic-sericeous abaxial leaf surface. Jussieu noted the fact that each of the four lateral sepals bore one large gland, instead of the paired glands found in most neotropical Malpighiaceae. When he published his monograph of the family in 1843, Jussieu gave a more complete description of the species and placed the genus in his tribe Banisterieae, which comprised genera with the dorsal wing dominant. He then went on to say that the affinity of the genus was doubtful, adding that it resembled several genera in some characters but other characters made all those relationships unlikely, and concluded with the curious suggestion that it was perhaps closest to Pterandra.


FIG. 1. Distribution of Lophopterys.

Niedenzu (1928) also placed Lophopterys among the neotropical genera with the dorsal wing dominant, in his subtribe Banisteriinae. The only material he saw was the Poiteau type, to which he gave the superfluous name $L$. splendens var. oblanceolata Nied., and two flowering collections from British Guiana [now Guyana] of what he called L. splendens var. obovata Nied.

In 1935 Kostermans described as the new genus Dolichopterys a species from Suriname, to which he gave the name D. surinamensis Kosterm. His material resembled Lophopterys splendens in most respects, but each mericarp of its fruit bore, in addition to the dorsal wing, two long narrow lateral wings toward the apex of the nut (Fig. 8b). Kostermans suggested that Dolichopterys [the name means "long-wing"] evolved from an ancestor in Tetrapterys or Triopterys that lost the lower lateral wing(s) found in those genera, and that Lophopterys was in turn derived from Dolichopterys through loss of the upper lateral wings, with only the dorsal crest retained.

Sandwith (1951) described as Lophopterys euryptera the taxon of British Guiana that Niedenzu had treated as L. splendens var. obovata. Sandwith had fruits, which resembled those of Dolichopterys surinamensis, so he knew that Niedenzu's assignment of the specimens from British Guiana to a variety of L. splendens was inappropriate. He argued that the fruit difference alone did not justify the recognition of two genera, so he proposed the combination L. surinamensis (Kosterm.) Sandwith. Thus, at that time the genus Lophopterys comprised three species, one endemic to each of the Guianas: L. euryptera in British Guiana, L. surinamensis in Suriname, and L. splendens in French Guiana. Sandwith discussed the possible
affinities of Lophopterys and generally supported Kostermans's comparison with Tetrapterys spp. because of the long narrow lateral wings on the samara, but cautioned that in other characters Lophopterys was so unlike Tetrapterys that the relationship was by no means certain.

In 1981 W. Anderson pointed out that Lophopterys euryptera occurs also in Venezuela, and provided a key to distinguish L. euryptera and L. surinamensis. Since then he has described two species from the interior of South America, L. inpana (1990b) and L. peruviana (1993). The present study adds descriptions of two new species and makes the first attempt to consider the genus as a whole since Sandwith's 1951 paper.

## MORPHOLOGY, CIRCUMSCRIPTION, AND SYSTEMATIC POSITION OF THE GENUS

The genus Lophopterys is unusually homogeneous in a whole suite of characters that are traditionally important in the systematics of the Malpighiaceae. The plants are mostly woody vines of lowland forests, with persistently sericeous stems. The lamina is always densely and persistently sericeous on the abaxial surface, a feature known in other neotropical Malpighiaceae but not generally so conserved across an entire group of closely related species. There are either no glands on the lamina or at most two small glands on the margin near the base. Stipules are mostly absent, and only vestigial when present. The flowers are always borne in elongated pseudoracemes, although the branching of the inflorescence varies. In most characters the flowers fit the standard pattern found in the large majority of climbing neotropical Malpighiaceae (W. Anderson 1979) -yellow petals, ten stamens without strong differentiation of the anthers, three carpels with separate styles which are stigmatic on the internal angle-and thus are not very informative about relationships of the genus. While the characters above, taken together, can help to identify the genus, they tell us relatively little about the position of the genus in the family. Below we shall discuss in more detail the calyx glands, pollen, and unique fruits, which one might reasonably expect to shed light on the origin and relationships of Lophopterys.

The most noteworthy apomorphy of Lophopterys, aside from the distinctive fruit, is the usual presence on each of the four lateral sepals of one very large, radially lineate gland, presumably the result of the complete fusion of the paired abaxial glands found on the lateral sepals of most neotropical Malpighiaceae. Those calyx glands are a constant feature of Lophopterys; the only exception is the few populations of L. inpana that have lost the glands entirely. Therefore, it seems likely that the ancestor of the genus already had such glands, and if such a rare apomorphy were to be shared with other clades one would hope to have that tell us which are likely to be the closest sister genera. There are, in fact, two other genera of Amazonian Malpighiaceae in which such partial to complete fusion of the calyx glands is common. One is Jubelina Adr. Juss. in Deless. (W. Anderson 1990a, 2001); the other is Mezia Schwacke ex Nied. in Engl. \& Prantl (W. Anderson 2001). All but one species of Jubelina have the calyx glands consistently completely connate, while the species of Mezia vary from having all the glands distinct to having them partially to completely connate. Unfortunately, in neither Jubelina nor Mezia do other aspects of the morphology support a close relationship to Lophopterys. In both, characters of vesture, leaf glands, inflorescences,
styles, and fruits are so different from Lophopterys that we must conclude that the fusion of the calyx glands probably occurred independently in the three genera (as is suggested by the existence of species with distinct glands in both Jubelina and Mezia). The calyx glands, while a very useful generic character for Lophopterys, do not seem to reveal anything about its position in the family.

The pollen of the Malpighiaceae falls into two broad classes, radially symmetrical (with the ectoapertures oriented at right angles to the equator) and globally symmetrical (without identifiable equator or poles and the apertures variously oriented). Previous authors have suggested that radially symmetrical pollen is plesiomorphic in the family, on the basis of the common occurrence of similar pollen in other rosid families (e.g., Lowrie 1982; W. Anderson 1990c), and a recent molecular study (Davis et al., in press) has confirmed that globally symmetrical pollen is derived in the family and evolved once. Lophopterys has the derived, globally symmetrical type of pollen, with 12 or more ectoapertures (rugae in the terminology of Lowrie) oriented more or less at right angles to each other, and typically with endoapertures (pores) associated with six of the rugae, but not necessarily in the center of the ruga and not in an obviously consistent pattern (Lowrie 1982; see our Fig. 2). Such pollen is what we would expect in Lophopterys, because almost all genera of wing-fruited vines have globally symmetrical pollen. However, Lowrie (1982, p. 120) stated that the specific characteristics of the pollen of Lophopterys were not informative in assessing its relationships within that very large clade, and we have to agree. The pollen in this genus reinforces its placement among the many genera of neotropical vines with winged fruits, but is otherwise uninformative.

With the exception of Lophopterys splendens, which is discussed separately below, the samaras are similar in all the species of Lophopterys. The nut is spheroidal; there is a large, inequilaterally trapezoidal dorsal wing with its greatest width toward the base of the nut; and there are two long, narrow lateral wings borne toward the apex of the nut and pointed upward (see, for example, Figs. 4 g and 5 g ). The lateral wings are oriented at an angle of about $45-60^{\circ}$ to the dorsal wing. The genus can be divided into a group of three species with large samaras (L. euryptera, L. peruviana, and L. surinamensis) and a group of three with small samaras (L. floribunda, L. inpana, and L. occidentalis), but except for size the samaras are qualitatively very much alike in all six species. That samara is unique in the family. The only genus with a samara resembling that of Lophopterys is Tetrapterys Cav., in which each samara bears four elongated lateral wings, with the upper two usually longer than the lower two. In some species of Tetrapterys the lower wings are much reduced, and in at least one (T. diptera Cuatrec., of Colombia) they are completely lost and the samara bears a strong superficial resemblance to that of Lophopterys. However, the single large calyx glands of Lophopterys are unknown in Tetrapterys, the dorsal wing, even when relatively large, never approaches the size or peculiar shape of that in Lophopterys, and in the group with fruits most like those of Lophopterys (section Tetrapterys) the inflorescence and stipules are wholly different. None of this rules out the possibility that Lophopterys and Tetrapterys shared a common ancestor with long narrow lateral wings, but nothing in the morphology except the samara's lateral wings supports that possibility.

The type of the genus, Lophopterys splendens, has a mericarp that is quite different from the samaras of the other species. The lateral wings are absent,


FIG. 2. Pollen of Lophopterys. a. L. occidentalis (Maguire et al. 56702). b. L. inpana (Morawetz \& Wallnöfer 13-10988). Scale $=10 \mu \mathrm{~m}$.
represented at most by ribs where they "should" be; the nut is ellipsoidal, not spheroidal; and the dorsal wing is a mere crest, rather than the large trapezoidal wing of the other species. The fruit is so different, in fact, that one can fairly ask whether we are correct to put them in the same genus; perhaps Kostermans was justified in erecting the genus Dolichopterys for the species with lateral wings. On the other hand, all the other characters of L. splendens-indument, inflorescence, calyx glands, androecium, and gynoecium-support a close relationship to the other species treated here, especially the species of the Guianas. We conclude that $L$. splendens is best treated with the group from which it very likely originated by reduction of the fruits, just as C. Anderson (1997) kept the segregate Brachypterys Adr. Juss. in Stigmaphyllon Adr. Juss.

Two recent molecular studies (Cameron et al., in press, and Davis et al., in press) sequenced two different pairs of chloroplast genes from material representing most of the genera of the Malpighiaceae to infer phylogenetic relationships within the family. Lophopterys was represented by L. floribunda, which was placed, but without significant support, as sister to a clade containing Malpighia, Mascagnia sens. str., Triopterys, and a group of Old World genera with lateral-winged samaras. There was no support in those trees for associating Lophopterys with Tetrapterys. The weak support for its placement as sister to the "malpighioids" suggests that Lophopterys may well move elsewhere in the family tree. Davis (unpublished) has recently assembled a phytochrome (PHYC) nuclear data set for the Malpighiaceae. The phytochrome gene family ( $P H Y B$ ) has been particularly informative within grasses (Mathews et al. 2000), resolving $67 \%$ of the nodes with bootstrap values of $>91 \%$. These data, when combined with the existing $n d h F$ data set, resolve many of the relationships among the enigmatic wing-fruited taxa. In these analyses, Lophopterys is weakly placed as sister to Hiraea fagifolia (DC.) Adr. Juss. in a well-supported clade (i.e., $80 \%$ bootstrap) that also includes Mascagnia hippocrateoides (Triana \& Planch.) Nied. and Mascagnia dipholiphylla (Small) Bullock. Placement with those taxa, all of which have a butterfly-shaped samara with two distinct lateral wings, seems much more reasonable than a putative relationship with Mascagnia sens. str. and its relatives, which have a single continuous lateral wing. This does not definitively resolve the problem of the position of Lophopterys among the neotropical wing-fruited clades, but 158 years after Jussieu first discussed the affinities of Lophopterys we are making significant progress toward solving the puzzle posed by this beautiful and distinctive little genus.

## TAXONOMY

Lophopterys Adr. Juss. in Deless., Icon. Sel. Pl. 3: 18. 1838.-Type: Lophopterys splendens Adr. Juss.
Dolichopterys Kosterm., Recueil Trav. Bot. Néerl. 32: 279. 1935.-Type: Dolichopterys surinamensis Kosterm. [=Lophopterys surinamensis (Kosterm.) Sandwith].

Woody lianas or shrubs (or small trees?); stems densely, tightly, and persistently sericeous and often flattened or quadrangular when young, sometimes glabrescent in later years and becoming terete through secondary growth. Leaves opposite or subopposite; lamina densely and persistently sericeous below, mostly eglandular, occasionally biglandular on margin at base; stipules absent or vestigial, $0.2-0.5 \mathrm{~mm}$ long, borne on adaxial edges of petiole $1-2 \mathrm{~mm}$ above base. Inflorescence paniculate, rarely simple, the flowers ultimately borne in pseudoracemes with the flowers proximally decussate but distally mostly in no regular order, sometimes decussate, sometimes in whorls of 3 or 4 ; bracts and bracteoles mostly eglandular and adaxially glabrous (except in some populations of L. inpana), the bracteoles borne at apex of peduncle when peduncle is developed. Flowers with pronounced bilateral symmetry. Sepals 5, abaxially sericeous or tomentose, adaxially glabrous, the anterior sepal eglandular, the 4 lateral sepals usually each bearing a single, very large, circular or transversely elliptical, radially lineate abaxial gland. Petals 5, yellow, glabrous or only very sparsely sericeous abaxially; lateral petals reflexed; posterior petal with the claw erect and the limb erect to reflexed. Receptacle glabrous. Stamens 10; filaments glabrous, longer opposite sepals than petals, erect and nearly straight to reflexed distally; anthers $\pm$ alike, the connective not enlarged distally, the locules parallel, linear, $\pm$ membranous along edges; pollen globally symmetrical, with 12 or more non-equatorial, polyhedrally disposed rugae and typically 6 pores randomly associated with some of the rugae. Ovary of 3 distinct carpels, 1 anterior and 2 posterior, all fertile, $1-1.5 \mathrm{~mm}$ high, densely sericeous; styles 3, stout, the anterior shorter than the posterior 2, the stigmas large, borne on internal angle of apex. Fruit breaking apart into 3 samaras borne on a short pyramidal torus, each bearing a relatively short, inequilaterally trapezoidal or flabellate dorsal wing with its greatest width toward base of nut and 2 long, narrow, forward-pointing lateral wings 3 or more times as long as wide (except $L$. splendens, which has a narrow dorsal crest and the lateral wings reduced to ridges or lost). Embryo spheroidal, with one cotyledon folded upward distally around the other, the inner cotyledon often also folded back on itself distally.

The measurements given below for the dorsal wing of the samara follow the convention used by W. Anderson in 1981 (p. 26), with "width" denoting the distance from the nut to the farthest margin and "height" the maximum measurement at right angles to the width.

## Key to the Species of Lophopterys, for Specimens with Flowers

[^0]1. Anther locules glabrous.
2. Peduncle $1-9 \mathrm{~mm}$ long; axis of pseudoraceme up to 2 mm in diameter in flower; pedicel up to 1.5 mm in diameter at apex.
3. Abaxial surface of dried lamina metallic-sericeous with a bronze to golden sheen; inflorescence axes reddish brown; peduncle $1.7-9 \mathrm{~mm}$ long; bracts and bracteoles strongly spreading; bracteoles $1.5-3 \mathrm{~mm}$ long, $1-2.3 \mathrm{~mm}$ wide. L. inpana.
4. Abaxial surface of dried lamina with a matte finish, the very tight vesture not obvious but giving a gray or silvery aspect; inflorescence axes golden or brown; peduncle 1-2 mm long; bracts and bracteoles appressed or spreading at apex; bracteoles $0.8-1 \mathrm{~mm}$ long, $0.5-1 \mathrm{~mm}$ wide.
L. peruviana.
5. Peduncle absent or up to 1 mm long in fruit; axis of pseudoraceme $1.5-4 \mathrm{~mm}$ in diameter in flower; pedicel at least 2 mm in diameter at apex.
6. Lamina abruptly acuminate at apex; bracts in distal half of pseudoraceme $2.7-5 \mathrm{~mm}$ long; pedicel $8-12 \mathrm{~mm}$ long. L. splendens.
7. Lamina broadly truncate or rounded to emarginate and often apiculate at apex; bracts in distal half of pseudoraceme $2-3 \mathrm{~mm}$ long; pedicel $3-8 \mathrm{~mm}$ long.
8. Petiole of larger leaves $20-60 \mathrm{~mm}$ long; lamina of larger leaves $10-23 \mathrm{~cm}$ wide, very tightly sericeous below. L. euryptera.
9. Petiole of larger leaves $15-20 \mathrm{~mm}$ long; lamina of larger leaves $8-10 \mathrm{~cm}$ wide, loosely sericeous below.
L. surinamensis.

## Key to the Species of Lophopterys, for Specimens with Fruits

1. Lateral wings absent from samara.
L. splendens.
2. Lateral wings present on samara.
3. Lateral wings of samara $45-62 \mathrm{~mm}$ long, $6.5-18 \mathrm{~mm}$ wide; dorsal wing of samara $10-20$ mm wide, $19-30 \mathrm{~mm}$ high; nut of samara $9-14 \mathrm{~mm}$ in diameter.
4. Petiole of larger leaves $20-60 \mathrm{~mm}$ long; lamina of larger leaves $10-23 \mathrm{~cm}$ wide, obovate; hairs on nut of samara white. L. euryptera.
5. Petiole of larger leaves $15-21 \mathrm{~mm}$ long; lamina of larger leaves $8-11 \mathrm{~cm}$ wide, obovate or elliptical; hairs on nut of samara stramineous to brown.
6. Lamina obovate, broadly rounded and deeply emarginate at apex, the abaxial vesture relatively loose; pseudoracemes $17-23 \mathrm{~cm}$ long, subvelutinous with the hairs dark brown; nut of samara $10-14 \mathrm{~mm}$ in diameter; bracts and bracteoles mostly deciduous in fruit. L. surinamensis.
7. Lamina elliptical, abruptly acuminate at apex, the abaxial vesture very tightly appressed; pseudoracemes 6-12.5 cm long, sericeous with the hairs golden or brown; nut of samara $9-10 \mathrm{~mm}$ in diameter; bracts and bracteoles persistent in fruit.
L. peruviana.
8. Lateral wings of samara $15-38 \mathrm{~mm}$ long, $4-9 \mathrm{~mm}$ wide; dorsal wing of samara $5-13 \mathrm{~mm}$ wide, $5-18 \mathrm{~mm}$ high; nut of samara $3.3-8 \mathrm{~mm}$ in diameter.
9. Bracts in distal half of pseudoraceme $2.5-8 \mathrm{~mm}$ long; bracteoles $1.5-3 \mathrm{~mm}$ long, spreading; pseudoracemes containing 2-28 flowers; sepals $2-3 \mathrm{~mm}$ long beyond gland; inner face of seed locule glabrous. L. inpana.
10. Bracts in distal half of pseudoraceme $0.5-1 \mathrm{~mm}$ long; bracteoles $0.5-1.1 \mathrm{~mm}$ long, ascending or appressed; pseudoracemes containing (15-) 25-100 or more flowers; sepals 1 1.5 mm long beyond gland; inner face of seed locule strigose.
11. Peduncle $0.5-2.5(-3) \mathrm{mm}$ long; pedicel $2-4 \mathrm{~mm}$ long; hairs brown or dark brown throughout the inflorescence.
L. floribunda.
12. Peduncle (2-) $2.5-4 \mathrm{~mm}$ long, with at least some peduncles in every inflorescence 2.5 mm long or longer; pedicel 3.3-5(-6) mm long; hairs golden-brown or golden on ultimate axes of inflorescence, especially peduncles and pedicels. L. occidentalis.

Lophopterys euryptera Sandwith, Kew Bull. 1951: 34. 1951. Lophopterys splendens var. obovata Nied. in Engl., Pflanzenr. IV, 141: 385. 1928.-Type: Guyana [British Guiana]. Barama River, Oct fl, Rich. Schomburgk 1536 (lectotype for both names, here designated: K !, the sheet with an inflorescence [WRA neg. 81-8-1]; isolectotype: K!).

Fig. 3.

Woody liana to 35 m long; stem hairs stramineous or brownish fading to gray. Lamina of larger leaves $16-35 \mathrm{~cm}$ long, $10-23 \mathrm{~cm}$ wide, obovate, truncate or shortattenuate and often unequal at base, plane at margin, very broadly truncate to emarginate and often apiculate at apex, eglandular, initially loosely sericeous above but eventually glabrate with pubescence rarely persistent along midrib, densely and persistently sericeous below with very tightly appressed hairs giving the dried leaf a silvery to golden sheen, the $8-16$ pairs of lateral veins prominent below, interconnected by prominulous parallel secondary veins, the intricate reticulum prominulous on both sides but hidden below by the vesture; petiole $20-60 \mathrm{~mm}$ long, persistently sericeous or glabrescent in age, eglandular or bearing $1-4$ pairs of small glands at various distances from base along adaxial edges; stipules not found. Inflorescence tightly to loosely sericeous with the hairs brown to rarely white, $10-30 \mathrm{~cm}$ long, terminal and axillary, a panicle with the pseudoracemes 516 cm long and containing 10-50 flowers, the axis $1.5-3 \mathrm{~mm}$ in diameter; bracts and bracteoles abaxially sericeous to glabrate, persistent in fruit, triangular, appressed; bracts $2-3 \mathrm{~mm}$ long (proximal bracts up to 10 mm long), $1-2(-3) \mathrm{mm}$ wide; peduncle absent or up to 1 mm long in fruit; bracteoles $1.5-2.5 \mathrm{~mm}$ long, $1-1.5$ mm wide; pedicel $3-8 \mathrm{~mm}$ long, $2-2.5 \mathrm{~mm}$ in diameter at apex, sericeous. Flowers erect or very slightly circinate in bud. Sepals triangular, $3-3.5 \mathrm{~mm}$ long ( $1-2 \mathrm{~mm}$ beyond gland), $2-3 \mathrm{~mm}$ wide, sometimes membranous at margin, acute to broadly obtuse at apex, abaxially sericeous, strongly appressed in anthesis; glands 1.5-2.5 mm long and $1.5-3 \mathrm{~mm}$ wide, transversely elliptical to circular, absent from one anterior-lateral sepal in some flowers. Petals glabrous; lateral petals with the claw $2.5-3.5 \mathrm{~mm}$ long, winged, the limb 5-6 mm long, $6-9 \mathrm{~mm}$ wide, concave, rotund or obovate, decurrent and weakly differentiated from the claw, erose and eglandular at margin; posterior petal with the claw $2.5-3 \mathrm{~mm}$ long, unwinged, not constricted at apex, the limb $3.5-4 \mathrm{~mm}$ long and wide, rectangular, flat and reflexed, fimbriate with the proximal fimbriae broadly glandular, the distal fimbriae finer and decreasingly glandular to eglandular. Filaments $2-3 \mathrm{~mm}$ long, connate in the proximal $0.5-1 \mathrm{~mm}$; anthers $1.5-2 \mathrm{~mm}$ long, $\pm$ alike, reflexed, glabrous. Styles glabrous or sericeous in the proximal half, the anterior style $2-2.5 \mathrm{~mm}$ long, straight or very slightly reflexed at apex, the posterior two $2.5-3 \mathrm{~mm}$ long, strongly reflexed distally, all with the stigmas much wider than high (ca. $0.5-0.8 \mathrm{~mm}$ wide, $0.2-0.3 \mathrm{~mm}$ high), dorsally rounded, truncate, or slightly apiculate at apex. Samara with the nut spheroidal, ca. $9-11 \mathrm{~mm}$ in diameter, smooth on sides or bearing obscure vertical ribs and smooth between wings, sericeous, the hairs white and persistent; lateral wings $45-62 \mathrm{~mm}$ long, $10-18 \mathrm{~mm}$ wide, narrowly elliptical and gradually tapered distally to a rounded or obtuse apex, sericeous to glabrate; dorsal wing encircling much of the nut, trapezoidal-flabellate, 10-19 mm wide, 19-25 mm high, entire or slightly erose, sericeous; ventral areole 4-6 mm high and wide, ovate; inner face of seed locule appressed-tomentose.

Phenology. Probably flowering and fruiting in all months
Distribution (Fig. 1). Central to northern Guyana and eastern Venezuela; lowland rainforests; 75-320 m.

Additional Specimens Examined. Guyana. Mahdia Creek, Potaro River, 107 miles on BarticaPotaro road, Jan fr, Fanshawe in Forest Dept. 3749 (K); Barima River, Mar fl, Jenman 6994 (K, NY); Barima-Waini Region, trail between Aranka Head and Barima Head, NW of Kariako River, $07^{\circ} 30^{\prime}$ N, $60^{\circ} 35^{\prime} \mathrm{W}, 76-122 \mathrm{~m}$, mixed forest, slopes and terraces, Apr fl, McDowell 4386 (MICH); upstream from Kariako Village, Barama River, North-West District, $07^{\circ} 22^{\prime} \mathrm{N}, 59^{\circ} 42^{\prime} \mathrm{W}, 145 \mathrm{~m}$, riparian forest, Jan ster, van Andel \& Samuels 906 (MICH). Venezuela. Bolivar: Alto Río Cuyuní, Río Uiri-yuk,


FIG. 3. Lophopterys euryptera. a. Leaf and inflorescence, $\times 0.5$. b. Flower, $\times 2.5$. c. Stamens, $\times 10$. d. Gynoecium, anterior style in center, $\times 7.5$. e. Samara, $\times 0.5$. (Based on: a-d, Breteler 3752; e, Maguire et al. 46977.)
along river, Aug fr, Maguire et al. 46977 (K, MICH, MY, NY, US, VEN).-Delta Amacuro: E of Río Grande, ENE of El Palmar, near Bolívar border, Jun/Jul fl/fr, Blanco 155 (VEN); near Bolívar border, $08^{\circ} 04^{\prime} \mathrm{N}, 61^{\circ} 44^{\prime} \mathrm{W}$, low primary forest, 320 m , Apr fl, Breteler 3752 (MER, MO, NY, U, US, VEN); E of Río Grande, directly E of El Palmar, swampy mature forest, Jul fr, Gentry \& Berry 14942 (MICH, MO); between La Margarita and Puerto Miranda, Río Acure, rainforest, 80-100 m, Nov fr, Steyermark 87776 (NY, VEN); E of Río Grande, 37 km ENE of El Palmar, rainforest, 320 m , Feb fr, Steyermark 93148 (NY, U, VEN).

This species is generally most like its nearest neighbor, L. surinamensis (see Fig. 1). Both have large samaras and sessile or subsessile pedicels, but L. euryptera is distinguished by its larger leaves and especially by its petioles, the longest in the genus.

Lophopterys floribunda W. R. Anderson \& C. C. Davis, sp. nov.-Type: Brazil. Minas Gerais: Manhuaçu, arredores, orla da mata, 15 Oct 1983 fl, G. Hatschbach \& O. Guimarães 46868 (holotype: MBM!; isotype: MICH!).

Liana lignosa vel frutex usque ad 1 m altus; lamina foliorum majorum 11-23 $(-26) \mathrm{cm}$ longa, $5-11(-13) \mathrm{cm}$ lata, apice $\pm$ abrupte breviacuminata vel rotundata vel obtusa breviapiculataque, petiolo $10-25 \mathrm{~mm}$ longo; pseudoracemi ex (25-) 40100 plusve floribus constantes; bracteae $0.5-1.5 \mathrm{~mm}$ longae; pedunculi pedicellique brunnei vel atrobrunnei, illi $0.5-2.5(-3) \mathrm{mm}$ longi, hi 2-4 mm longi; bracteolae $0.5-1.1 \mathrm{~mm}$ longae, $\pm$ appressae; sepala glandulas $1-1.5 \mathrm{~mm}$ superantia; antherae pilosae; nux samarae 4-6 mm diametro, alae laterales $25-35 \mathrm{~mm}$ longae, $6-9 \mathrm{~mm}$ latae, ala dorsalis $6-11 \mathrm{~mm}$ lata, $10-18 \mathrm{~mm}$ alta, loculus intus strigosus.

Woody liana or shrub 1 m tall; stem hairs ferrugineous fading to gray. Leaves opposite or subopposite; lamina of larger leaves 11-23 (-26) cm long, 5-11 (-13) cm wide, narrowly to broadly elliptical, cuneate, obtuse, or rounded at base, nearly or quite plane at margin, $\pm$ abruptly short-acuminate at apex to rounded or obtuse and short-apiculate, eglandular, sericeous above to usually glabrate in age or persistently sericeous on midrib, especially proximally (occasionally $\pm$ persistently sericeous all over adaxial surface), densely and persistently sericeous below, the hairs very short and tightly appressed, all the same color or slightly darker on midrib and lateral veins, giving the dried leaf a silvery, golden, or bronze metallic sheen, the 8-13 pairs of lateral veins prominent below, the intricate reticulum usually prominulous on both sides; petiole $10-25 \mathrm{~mm}$ long, persistently sericeous, eglandular or bearing 1-7 pairs of small glands embedded in adaxial edges; stipules not found. Inflorescence tightly brown- or dark-brown-sericeous, 13-30 cm long, terminal and axillary, paniculate, the pseudoracemes $5-21 \mathrm{~cm}$ long and containing (25-) $40-100$ or more flowers, the axis $0.8-1.5 \mathrm{~mm}$ in diameter; bracts and bracteoles abaxially thinly to densely sericeous, persistent, triangular, ascending or appressed; bracts $0.5-1.5 \mathrm{~mm}$ long and wide; peduncle $0.5-2.5(-3) \mathrm{mm}$ long; bracteoles $0.5-$ 1.1 mm long and wide; pedicel $2-4 \mathrm{~mm}$ long, $0.9-1.5 \mathrm{~mm}$ in diameter at apex. Flowers slightly circinate to erect in bud. Sepals ovate or triangular, $1.5-2 \mathrm{~mm}$ long ( $1-1.5 \mathrm{~mm}$ beyond gland), $1.2-2 \mathrm{~mm}$ wide, often membranous and slightly revolute at margin, broadly obtuse or rounded at apex, abaxially brown- or gold-en-brown-sericeous, appressed in anthesis; glands $1-1.8 \mathrm{~mm}$ long, $1.5-2.3 \mathrm{~mm}$ wide, occasionally circular but mostly transversely elliptical. Lateral petals glabrous or very sparsely sericeous abaxially in the center, the claw $0.5-1 \mathrm{~mm}$ long, winged, the limb $5.5-8.5 \mathrm{~mm}$ long, $5.5-9 \mathrm{~mm}$ wide, somewhat concave to flat, obovate, erose or dentate and eglandular at margin; posterior petal glabrous, the claw very thick, $2.5-3 \mathrm{~mm}$ long, unwinged, usually $\pm$ constricted at apex, the limb
$2.5-3 \mathrm{~mm}$ long and wide, orbicular or rectangular, $\pm$ crumpled, erect to reflexed, dentate or short-fimbriate with the divisions all eglandular or the proximal ones slightly glandular-thickened. Filaments $1.5-3 \mathrm{~mm}$ long, $1 / 3-2 / 3$-connate; anthers $0.9-1.2 \mathrm{~mm}$ long, $\pm$ similar, erect or reflexed, the locules loosely pilose. Styles sericeous at base, $1.2-2 \mathrm{~mm}$ long, divergent to strongly spreading, dorsally rounded at apex, terete or laterally flattened, the stigmas orbicular or vertically to horizontally elliptical. Samara with the nut spheroidal, 4-6 mm in diameter, smooth on sides or bearing many obscure to prominent vertical ribs and smooth to irregularly rugulose between lateral and dorsal wings, sericeous or subvelutinous, the hairs brown; lateral wings $25-35 \mathrm{~mm}$ long, $6-9 \mathrm{~mm}$ wide, narrowly elliptical and obtuse or rounded (rarely acute) at apex, sericeous; dorsal wing encircling much of the nut, trapezoidal, $6-11 \mathrm{~mm}$ wide, $10-18 \mathrm{~mm}$ high, entire or erose, sericeous; ventral areole 2.5-3.5 mm high and wide, ovate; inner face of seed locule strigose.

Phenology. Collected with flowers from July to December, most commonly in September, and with fruits from September to December.

Distribution (Fig. 1). Central to eastern Amazonian Brazil and southeastern Brazil where Bahia, Espírito Santo, and Minas Gerais come together; edge of wet forest on terra firme, at low elevations, up to 620 m .

Additional Specimens Examined. Brazil. Amapá: Mpio. Calçoene, 53-72 km WNW of Calçoene, $02^{\circ} 33-38^{\prime} \mathrm{N}, 51^{\circ} 16^{\prime} \mathrm{W}$, Dec fl/imm fr, Rabelo et al. 2966 (MG, MICH, ULM).—Amapá/Pará: Rio Jarí, Monte Dourado, Planalto B, entre Pilão e Repartimento, Oct fl, N. T. Silva 1324 (MICH, NY).Amazonas: Estrada Manaus-Caracaraí, Km 57, Sep bud, Damião 699 (INPA).-Bahia: 5 km W of Itamaraju, Sep bud, Mori et al. 10746 (CEPEC, MICH).-Espírito Santo: Santa Teresa, estrada de Tabocas para Várzea Alegre, 550 m , Nov fl/fr, Kollmann 926 (MICH).-Minas Gerais: Mpio. Marliéria, Parque Estadual do Rio Doce, $19^{\circ} 46^{\prime} \mathrm{S}, 42^{\circ} 36^{\prime} \mathrm{W}, 450 \mathrm{~m}$, Sep fl, Heringer \& Eiten 15099 (MICH, MO); Parque Estadual do Rio Doce, Marliéria, início da trilha do Vinhático, $19^{\circ} 45^{\prime} 95^{\prime \prime} \mathrm{S}$, $42^{\circ} 37^{\prime} 38^{\prime \prime}$ W, Sep fl, Lombardi 1981 (MICH); Estação Biológica da Caratinga, fazenda Montes Claros, Caratinga, $19^{\circ} 43^{\prime} 53^{\prime \prime} \mathrm{S}$, $41^{\circ} 49^{\prime} 02^{\prime \prime}$ W, Sep fl, Lombardi 2357 (MICH); Jequeri, Nov fr, Salino 3805 (MICH).—Pará: Near Breu Branco, ca. 30 km N of Tucuruí, Feb ster, Anderson 13754 (MICH); Parauapebas, Reserva Biológica da Serra dos Carajás, 620 m , Jan ster, dos Santos et al. 419 (MICH); Tucuruí, PA-149, Oct fl, Lima \& A. Silva 04 (INPA, NY); Marabá, Carajás, Serra Norte, PA-275, Aug fl, Maciel et al. 729 (NY); Tucuruí, PA-149, Oct fl, Miranda et al. 682 (INPA, NY); Rio Itacaiunas, afl. do R. Tocantins, Serra Buritirama, Marabá, $05^{\circ} 30^{\prime}$ S, $50^{\circ} 15^{\prime} \mathrm{W}$, Jul bud, Murça Pires \& Belém 12586 (IAN, MICH); Tucuruí, Rio Tocantins, foz do Rio Pitinga, Sep fl/fr, Ramos \& Lima 1544 (INPA); Serra dos Carajás, 13 km from AMZA headquarters, road to sawmill, Oct fl/fr, A. S. Silva 71 (MICH, MG); Serra dos Carajás, Aug fl, N. T. Silva \& Ribeiro 3587 (MICH).

This species comprises, with L. occidentalis, a widespread and variable complex defined by the many-flowered pseudoracemes (hence the epithet floribunda), pilose anthers, and small samaras. The populations of that complex fall into three geographic ranges, including a group in southwestern Amazonia (described below as L. occidentalis), a group in central and eastern Amazonia, and a group in southeastern Brazil where Minas Gerais, Espírito Santo, and Bahia come together (Fig. 1). The latter two groups are treated here as the single species L. floribunda, in spite of the fact that the southern populations tend to have shorter pseudoracemes with darker vesture than the more northern populations. We are unable at this time to find stable differences that would allow us to distinguish the northern and southern populations in a defensible way. We offer this two-species resolution of the complex with some diffidence-it may well be that future workers will prefer to treat the whole complex as one variable species, or they may find bases for formal taxonomic recognition of all three geographical entities.

Lophopterys inpana W. R. Anderson, Contr. Univ. Michigan Herb. 17: 46. 1990.Type: Brazil. Rondônia: Summit of Serra dos Pacaás-Novos, 12 km NNE of Guajará-Mirim, 400 m , Aug fl, G. T. Prance et al. 6675 (holotype: INPA!; isotypes: MG! MICH! MO! NY! US!).

Figs. 2b, 4.
Woody liana or shrub up to 4 m tall; stem hairs initially reddish brown but sometimes fading to gray. Lamina of larger leaves $8.9-19.8 \mathrm{~cm}$ long, $3.4-10 \mathrm{~cm}$ wide, ovate or elliptical, cuneate or rounded at base, plane or slightly revolute at margin, sometimes short-acuminate but mostly acute or obtuse to rounded and often apiculate at apex, eglandular or occasionally bearing 2 small glands on margin at base, initially sericeous above but soon or eventually glabrate with pubescence occasionally persistent along midrib and margins and rarely on lamina, densely and persistently sericeous below with very tightly appressed hairs giving the dried leaf a bronze to golden metallic sheen, the 7-9 (-12) pairs of lateral veins prominent below, the intricate reticulum prominulous on both sides but hidden below by the vesture; petiole $10-18(-22) \mathrm{mm}$ long, persistently sericeous, eglandular or bearing $1-3$ pairs of small glands at middle or at various distances above or below middle along adaxial edges; stipules absent or vestigial, ca. 0.2 mm long, borne on adaxial edges of petiole $1-2 \mathrm{~mm}$ above base. Inflorescence sericeous with the hairs reddish brown, (4.5-) 6-24 cm long, terminal and axillary, racemose or paniculate, the pseudoracemes $2-12(-13.8) \mathrm{cm}$ long and containing 2-28 mostly decussate flowers, the axis $0.7-1.5 \mathrm{~mm}$ in diameter; bracts and bracteoles abaxially sericeous, adaxially thinly sericeous or glabrous, mostly persistent in fruit, spreading, often bearing 2 tiny glandular spots at abaxial base (especially bracts); bracts $2.5-8 \mathrm{~mm}$ long (proximal bracts up to 16.3 mm long), $1-$ 2 mm wide, narrowly triangular; peduncle $1.7-9 \mathrm{~mm}$ long; bracteoles $1.5-3 \mathrm{~mm}$ long, $1-2.3 \mathrm{~mm}$ wide, with the reticulum often visible on adaxial surface, mostly ovate or elliptical to rotund; pedicel $3.5-14 \mathrm{~mm}$ long, $0.7-1.4 \mathrm{~mm}$ in diameter at apex, sericeous. Flowers slightly circinate in bud. Sepals elliptical, 3-4 mm long ( $2-3 \mathrm{~mm}$ beyond gland), $1.6-2.5 \mathrm{~mm}$ wide, often membranous and slightly revolute at margin, broadly rounded at apex, abaxially sericeous, appressed in anthesis, often becoming somewhat spreading and more revolute at margin in fruit; glands 1.4-2.4 mm long and 1.8-3.4 mm wide, circular or more often transversely elliptical and sometimes emarginate at apex or at apex and base, rarely absent from all sepals. Petals usually glabrous, rarely sparsely sericeous abaxially on limb; lateral petals with the claw 1.5-3.6 (-4.4) mm long, winged, the limb 6-11 mm long, (6.2-) $7-12 \mathrm{~mm}$ wide, somewhat concave to flat, rotund or obovate, erose or dentate to short-fimbriate and eglandular at margin; posterior petal with the claw $3-4.2 \mathrm{~mm}$ long, unwinged, not constricted at apex, the limb (4.2-) 5.4-7 mm long, $4.3-7.5 \mathrm{~mm}$ wide, obovate, flat, erect to reflexed, fimbriate to lacerate with the proximal divisions sometimes fleshy or glandular. Filaments $2.2-3 \mathrm{~mm}$ long, basally connate; anthers $1-1.5(-2.2) \mathrm{mm}$ long, alike, erect or reflexed, glabrous. Styles sericeous on proximal half, $2-3 \mathrm{~mm}$ long, erect to divergent, dorsally rounded at apex, the stigmas obovate and decurrent. Samara with the nut spheroidal, 3.5-4.5 ( -6 ) mm in diameter, smooth on sides and between wings, sericeous, the hairs golden to whitish and persistent or unevenly deciduous; lateral wings 1523 ( -26 ) mm long, 4-7 mm wide, narrowly elliptical or slightly obovate with the margins parallel to divergent distally, more or less abruptly narrowed to the rounded or obtuse apex, sericeous to glabrate; dorsal wing $1 / 2-2 / 3$-encircling the nut, trapezoidal, 5-12 (-13) mm wide, (5-) 7-9 mm high, the upper margin irregularly


FIG. 4. Lophopterys inpana. a. Flowering branch, $\times 0.5$. b. Distal portion of petiole enlarged to show glands, $\times 5$. c. Unit of the inflorescence enlarged to show spreading bracts and bracteoles, $\times 2$. d. Flower, with posterior petal uppermost, $\times 2$. e. Stamens, abaxial view (left) and adaxial view (right), $\times 10$. f. Gynoecium, $\times 10$. g. Immature samara, $\times 1.5$. (Based on: a-c, Prance $6675 ;$ d-g, Killeen 2750.)
sinuous, sericeous to glabrate; ventral areole $2-2.5 \mathrm{~mm}$ in diameter, broadly ovate or rotund; inner face of seed locule glabrous.

Phenology. Collected with flowers in January, June, and especially August, September, and October, and with fruits in September, October, and November.

Distribution (Fig. 1). Central Amazonian Brazil to western Amazonia, from southern Venezuela to Peru, Bolivia, and Rondônia, Brazil; occasionally in wet forest, but mostly in more open places, such as low forest, thickets, or savannas; 50-800 m.

Additional Specimens Examined. Bolivia. Beni: Between Guayaramerín and Cachuela Esperanza, savanna and low, seasonally flooded woods, Sep fl, Michel \& Capra 2346, 2370 (MICH).Santa Cruz: Velasco Province, Parque Nacional Noel Kempf, $13^{\circ} 36^{\prime}-14^{\circ} 40^{\prime} \mathrm{S}, 60^{\circ} 40-54^{\prime} \mathrm{W}$, low dry forest, rocky campo, open savanna, edge of pampa and forest, Nov fr, Foster 14006 (F, MICH), Aug fl,

Guillén et al. 4159 (MICH), Oct fl/imm fr, Killeen 2750 (F, MICH, NY), Oct fr, Killeen 5851 (MICH), Aug fl, Toledo 37 (F), Sep fr, Vargas 3950 (MICH), Oct fl/fr, Vargas 3998 (CTES, MO), 4053 (F, MO). Brazil. Amazonas: Distr. Agropecuário, Reserva 1501 (Km 41) da WWF/INPA Projeto da Dinâmica Biológica dos Fragmentos Florestais, $02^{\circ} 25^{\prime} 31^{\prime \prime}-26^{\prime} \mathrm{S}, 59^{\circ} 43^{\prime} 40^{\prime \prime}-45^{\prime} 50$ " W, terra firme, Aug fl, Lepsch da Cunha et al. 296 (MICH, MO, NY); Km 65-70, Manaus-Itacoatiara, Oct fl, Oliveira 2752 (UB); Reserva Florestal Ducke, Manaus-Itacoatiara Km 26, 02 ${ }^{\circ} 53^{\prime} \mathrm{S}, 59^{\circ} 58^{\prime} \mathrm{W}$, Sep fl, Sothers 162 (MICH); Humaitá, Estrada Humaitá-Jacareacanga, Km $64-70,07^{\circ} 45^{\prime} \mathrm{S}, 62^{\circ} 32^{\prime} \mathrm{W}$, roadside thicket, Jun fl, Teixeira et al. 1124 (INPA, K, MG, MICH, MO). Peru. Huánuco: Pachitea Province, region of Pucallpa, W part of the Sira Mountains and adjacent lowland, $20-24 \mathrm{~km}$ SE of Puerto Inca, $09^{\circ} 28^{\prime} \mathrm{S}$, $74^{\circ} 47^{\prime} \mathrm{W}$, primary mountain rain forest, Morawetz \& Wallnöfer 11-27888 (Aug fl), 11-41088 (Oct fr), 13-10988 (Sep fl), 13-28888 (Aug fl) (all MICH). Venezuela. Amazonas: Depto. Atabapo, ca. 15 km SE of San Fernando de Atabapo, $03^{\circ} 55^{\prime} \mathrm{N}, 67^{\circ} 40^{\prime} \mathrm{W}$, bosque muy húmedo de tierra firme, Jan fl/imm fr, Stergios et al. 11604 (MICH, MO).

The small fruits of this species immediately distinguish it from most species of Lophopterys. The only other species with such small samaras are L. floribunda and L. occidentalis, both of which have hairy anthers. Lophopterys inpana is also notable for its relatively long, spreading bracts and bracteoles.

Lophopterys occidentalis W. R. Anderson \& C. C. Davis, sp. nov.-Type: Brazil. Acre: 12 km from Rio Branco on Rio Branco-Pôrto Velho road, disturbed primary forest, Sep f1/imm fr, S. R. Lowrie et al. 293 (holotype: INPA!; isotypes: INPA! MG! MICH! NY!).

Figs. 2a, 5.
Liana lignosa vel frutex usque ad 1 m altus; lamina foliorum majorum 11-18.5 cm longa, $5.5-8 \mathrm{~cm}$ lata, apice $\pm$ abrupte breviacuminata vel rotundata vel obtusa breviapiculataque, petiolo $10-19 \mathrm{~mm}$ longo; pseudoracemi ex (15-) $25-80$ floribus constantes; bracteae $0.8-1.1 \mathrm{~mm}$ longae; pedunculi pedicellique aurei vel aureobrunnei, illi (2-) $2.5-4 \mathrm{~mm}$ longi, hi $3.3-5(-6) \mathrm{mm}$ longi; bracteolae $0.6-1 \mathrm{~mm}$ longae, $\pm$ appressae; sepala glandulas $1-1.5 \mathrm{~mm}$ superantia; antherae pilosae; nux samarae $3.5-4.5 \mathrm{~mm}$ diametro, alae laterales $21-30 \mathrm{~mm}$ longae, $7-9 \mathrm{~mm}$ latae, ala dorsalis $6-10 \mathrm{~mm}$ lata, $7-13 \mathrm{~mm}$ alta, loculus intus strigosus.

Woody liana or shrub 1 m tall; stem hairs ferrugineous fading to gray. Leaves opposite or subopposite; lamina of larger leaves $11-18.5 \mathrm{~cm}$ long, $5.5-8 \mathrm{~cm}$ wide, elliptical or slightly ovate, cuneate, obtuse, or rounded at base, nearly or quite plane at margin, $\pm$ abruptly short-acuminate at apex to rounded or obtuse and short-apiculate, eglandular, sericeous above to glabrate in age or persistently sericeous on midrib, especially proximally, densely and persistently sericeous below, all the hairs very short and tightly appressed, brown on and near midrib and lateral veins and lighter in other areas, giving the dried leaf a light bronze metallic sheen, the (6-) 8-13 pairs of lateral veins prominent below, the intricate reticulum $\pm$ prominent above, prominulous below; petiole $10-19 \mathrm{~mm}$ long, persistently sericeous, eglandular or bearing $1-5$ pairs of small glands embedded in adaxial edges; stipules not found. Inflorescence tightly brown-sericeous on main axes, more loosely sericeous to subvelutinous on ultimate branches, peduncles, and pedicels with the hairs golden-brown or golden, 12-21 cm long, terminal and axillary, paniculate, the pseudoracemes (3-) 5-16 cm long and containing (15-) 25-80 flowers, the axis $0.8-1 \mathrm{~mm}$ in diameter; bracts and bracteoles abaxially sericeous, persistent or irregularly deciduous in fruit, narrowly triangular, ascending or appressed; bracts $0.8-1.1 \mathrm{~mm}$ long, $0.5-0.8 \mathrm{~mm}$ wide; peduncle (2-) $2.5-4 \mathrm{~mm}$ long (at least some in every inflorescence 2.5 mm long or longer); bracteoles $0.6-1 \mathrm{~mm}$ long, $0.4-0.8 \mathrm{~mm}$


FIG. 5. Lophopterys occidentalis. a. Flowering and fruiting branch, $\times 0.5$. b. Flower bud and adjacent portion of inflorescence, $\times 4$. c. Flower, side view, $\times 3$, and posterior petal, adaxial view, $\times 5$. d. Anthers, abaxial view (left) and adaxial view (right), $\times 15$. e. Gynoecium, anterior style to left, $\times 10$. f. Style tip, adaxial view, $\times 15$. g. Samaras, side view (left) and abaxial view (right), both $\times 1$. (Based on Lowrie et al. 293.)
wide; pedicel $3.3-5(-6) \mathrm{mm}$ long, $0.7-1.2 \mathrm{~mm}$ in diameter at apex. Flowers slightly circinate to erect in bud. Sepals ovate or elliptical, $1.3-2 \mathrm{~mm}$ long ( $1-1.5 \mathrm{~mm}$ beyond gland), $1.4-1.7 \mathrm{~mm}$ wide, often membranous and slightly revolute at margin, broadly obtuse or rounded at apex, abaxially golden-sericeous, appressed in anthesis, often becoming somewhat spreading and more revolute at margin in fruit; glands $1-1.5 \mathrm{~mm}$ long, $1.5-2 \mathrm{~mm}$ wide, transversely elliptical. Petals glabrous; lateral petals with the claw $0.5-1.3 \mathrm{~mm}$ long, winged, the limb $4-6.5 \mathrm{~mm}$ long, 4-6 mm wide, somewhat concave to flat, obovate, sinuate or erose to dentate and eglandular at margin; posterior petal with the claw very thick, $2.5-3.5 \mathrm{~mm}$ long, unwinged, $\pm$ constricted at apex, the limb $2-2.7 \mathrm{~mm}$ long, $1.3-2.9 \mathrm{~mm}$ wide, orbicular or rectangular, $\pm$ crumpled, erect to reflexed, fimbriate proximally with the divisions sometimes fleshy or glandular. Filaments $1.5-2.5 \mathrm{~mm}$ long, $1 / 3-1 / 2-$ connate; anthers ( $0.6-$ ) $0.8-1.2 \mathrm{~mm}$ long, subsimilar, erect or reflexed, the locules loosely pilose. Styles sericeous on proximal half, $1.5-2 \mathrm{~mm}$ long, divergent, dorsally rounded at apex, laterally $\pm$ flattened, the stigmas orbicular to vertically elliptical. Samara with the nut spheroidal or short-cylindroidal, $3.5-4.5 \mathrm{~mm}$ in diameter, with many vertical ribs on sides and irregularly rugulose between lateral and dorsal wings, sericeous or subvelutinous, the hairs stramineous; lateral wings 2130 mm long, $7-9 \mathrm{~mm}$ wide, narrowly elliptical or obovate and obtuse or rounded at apex, sericeous; dorsal wing encircling much of the nut, trapezoidal, $6-10 \mathrm{~mm}$ wide, $7-13 \mathrm{~mm}$ high, entire, sericeous; ventral areole $2.5-3 \mathrm{~mm}$ high and wide, ovate; inner face of seed locule strigose.

Phenology. Collected with flowers in September, and with fruits in late September, October, and November.

Distribution (Fig. 1). Southwestern Amazonian Brazil and adjacent Bolivia; wet primary or secondary forest on terra firme, at elevations up to 200 m .

Additional Specimens Examined. Bolivia. Beni: Vicinity of the Chácobo village Alto Ivon, $11^{\circ} 45^{\prime} \mathrm{S}, 66^{\circ} 02^{\prime} \mathrm{W}$, Nov fr, Boom 4035 (MICH, NY).-Pando: Prov. Madre de Dios, camino de Sena hacia el Río Beni, Oct fr, Beck et al. 20377 (MICH). Brazil. Amazonas: Track from Bôca do Acre airstrip to Monte Verde, north bank of Rio Purus, Sep fl, Prance et al. 2468 (INPA, MG, MICH, NY).-Rondônia: Km 8-23, Pôrto Velho, Sep fl, Maguire et al. 56702 (MICH, NY).

Our epithet for this species refers to its distribution, well to the west of the other populations in the Lophopterys floribunda/occidentalis complex. See discussion under L. floribunda.

Lophopterys peruviana W. R. Anderson, Contr. Univ. Michigan Herb. 19: 376. 1993.-Type: Peru. Amazonas: Alrededor de yucui entsa 6 horas de pongo del camino de Kusu, monte, 360-600 m, 12 Mar 1973 fr, R. Kayap 569 (holotype: MICH!; isotypes: F ! MO!).

Fig. 6.
Woody liana climbing to 25 m ; stem hairs initially golden-brown but usually fading to gray. Lamina of larger leaves $15-22.5 \mathrm{~cm}$ long, $8.5-11 \mathrm{~cm}$ wide, elliptical, rounded or cuneate at base, plane at margin, abruptly acuminate at apex, eglandular or occasionally biglandular on margin at base, initially sericeous above to very soon glabrate with pubescence often persistent along midrib and occasionally on lamina, densely and persistently sericeous below with very short and tightly appressed hairs giving the dried leaf a gray or silvery aspect, the 7-9 pairs of lateral veins prominent below, interconnected by prominulous parallel secondary


FIG. 6. Lophopterys peruviana. a. Fruiting branch, $\times 0.5$. b. Enlargement of adaxial surface of lamina to show scalariform crossveins, $\times 2.5$. c. Samaras, abaxial view (left) and side view (right), $\times 0.75$. d. Embryos, whole (right) and in longitudinal section (left), $\times 3$. e. Flower bud, $\times 5$. f. Flower, side view, with erect posterior petal, $\times 4$. g. Anther, abaxial view, $\times 15$. h. Gynoecium, anterior style in center, $\times 10$. i. Style tip, adaxial view, $\times 15$. (Based on: a-d, Kayap 569; e-i, Klug 654.)
veins, the intricate reticulum prominulous on both sides; petiole $16-21 \mathrm{~mm}$ long, persistently sericeous, eglandular or usually bearing a pair of large glands on adaxial edges near apex and sometimes a second more proximal pair as well, or bearing 1-4 pairs of small glands on the distal half; stipules absent or vestigial, $0.2-0.5 \mathrm{~mm}$ long, borne on adaxial edges of petiole $1-2 \mathrm{~mm}$ above base. Inflorescence densely and persistently sericeous with the hairs golden or brown, $11-20 \mathrm{~cm}$ long, paniculate, the pseudoracemes $6-12.5 \mathrm{~cm}$ long and containing $15-60$ flowers, the axis $1.4-2 \mathrm{~mm}$ in diameter; bracts and bracteoles abaxially sericeous to glabrate, persistent in fruit, appressed or spreading distally; bracts $1.5-3 \mathrm{~mm}$ long, $0.8-1.5 \mathrm{~mm}$ wide, narrowly triangular or triangular; peduncle $1-2 \mathrm{~mm}$ long; bracteoles like bracts but only $0.8-1 \mathrm{~mm}$ long, $0.5-1 \mathrm{~mm}$ wide, triangular or ovate; pedicel $4-7 \mathrm{~mm}$ long, 1.5 mm in diameter at apex, sericeous. Flowers slightly circinate to erect in bud. Sepals ovate, ca. 1 mm long beyond gland, $1.5-2 \mathrm{~mm}$ wide, broadly obtuse to rounded, abaxially densely sericeous to glabrescent, appressed in anthesis; glands $2-3.5 \mathrm{~mm}$ in diameter, circular. Petals glabrous; open flowers with intact lateral petals not seen; posterior petal ca. 6 mm long, obovate, the limb long-decurrent on the claw, toothed with the proximal teeth glandular. Filaments 1.52 mm long, up to $1 / 3$-connate; anthers $1.3-1.5 \mathrm{~mm}$ long, alike, erect to reflexed, glabrous. Styles sericeous their entire length, ca. 1.5 mm long, erect to divergent distally, dorsally rounded at apex, the stigmas transversely elliptical, much wider than high, and slightly decurrent. Samara with the nut spheroidal, $9-10 \mathrm{~mm}$ in diameter, smooth or slightly rugulose with the texture hidden by hairs, sericeous or appressed-tomentose, the hairs brown; lateral wings $45-50 \mathrm{~mm}$ long, $10-15 \mathrm{~mm}$ wide, narrowly elliptical and gradually tapered distally to an obtuse or rounded apex, sericeous; dorsal wing encircling much of the nut, trapezoidal, $10-20 \mathrm{~mm}$ wide, $20-30 \mathrm{~mm}$ high, entire or slightly sinuous, sericeous; ventral areole $5-6 \mathrm{~mm}$ high, 4 mm wide, ovate to nearly rotund; inner face of seed locule very sparsely sericeous.

Phenology. Collected with flowers in December, and with fruits in December and March.

Distribution (Fig. 1). Endemic to Peru; forest; 100-600 m.

Additional specimens examined. Peru. Loreto, Maynas Province: Mishuyacu near Iquitos, forest, Dec fl, Klug 654 (F, NY, US); Km 44, carretera Iquitos-Nauta, bosque primario, Dec fr, Vásquez \& Jaramillo 11420 (MICH).

The single flowering collection (Klug 654) differs in several respects from the two fruiting collections. Its bracts are narrow and gradually tapered, the inflorescence hairs are golden, and the petiole bears only very small glands, like those seen in other species of the genus. The fruiting collections have shorter, ovate, obtuse bracts and bracteoles, brown inflorescence hairs, and one or two pairs of large glands near the apex of the petiole. Those three collections may represent two different species, but we hesitate to try to distinguish them now because we do not have material in comparable stages of development. We are also influenced by the fact that Klug 654 and one of the fruiting collections, Vásquez \& Jaramillo 11420, came from the same area. When more and better collections become available it may be possible to refine the taxonomy proposed here.

When describing this species, one of us (WRA) stated that the anthers are sparsely sericeous between the locules. After re-examining the same specimens we cannot confirm the presence of those hairs.

Lophopterys splendens Adr. Juss. in Deless., Icon. Sel. Pl. 3: 18, pl. 29. 1838. Lophopterys splendens var. oblanceolata Nied. in Engl., Pflanzenr. IV, 141: 385. 1928, nom. superfl.-Type: French Guiana. Without locality, fr, Poiteau s.n. (holotype: G!; isotypes: $\mathrm{B} \dagger$ [F neg. 12750], G! K! [WRA negs. 91-1-20, 21], P-JU 11542! [WRA neg. 81-15-18]).

Fig. 7.
Woody liana or small tree 6 m tall; stem hairs golden or stramineous fading to gray. Lamina of larger leaves $16-\mathrm{ca} .27 \mathrm{~cm}$ long, $5.2-12.6 \mathrm{~cm}$ wide, elliptical to obovate, cuneate at base, nearly plane at margin, abruptly acuminate at apex, eglandular, glabrate above at maturity or persistently sericeous on midrib, especially proximally, densely and persistently sericeous below with an underlayer of very short, tightly appressed hairs and an overlayer of fewer, much longer, somewhat looser hairs, the aggregate giving the dried leaf a golden or bronze sheen, the 9-13 pairs of lateral veins prominent below, the intricate reticulum prominulous on both sides; petiole (11-) $12-22 \mathrm{~mm}$ long, persistently sericeous, eglandular or bearing 1-5 pairs of small glands in the middle third on adaxial edges; stipules not found. Inflorescence loosely sericeous to subvelutinous with the hairs brown or stramineous to gray, $15-45 \mathrm{~cm}$ long, terminal and axillary, racemose or paniculate, the pseudoracemes $5-26 \mathrm{~cm}$ long and containing 8-70 flowers, the axis 2-3.5 mm in diameter; bracts and bracteoles abaxially loosely sericeous, persistent or irregularly deciduous in fruit, narrowly triangular, appressed; bracts $2.7-5 \mathrm{~mm}$ long, $1-1.9 \mathrm{~mm}$ wide; peduncle absent or up to 1 mm long in fruit; bracteoles 1.4 2.2 mm long, $0.6-1 \mathrm{~mm}$ wide; pedicel $8-12 \mathrm{~mm}$ long, $2-2.8 \mathrm{~mm}$ in diameter at apex, loosely sericeous to subvelutinous. Flowers erect in bud. Sepals triangular, $3.5-4.5 \mathrm{~mm}$ long ( $1.5-2.1 \mathrm{~mm}$ beyond gland), $2.5-3.5 \mathrm{~mm}$ wide, plane at margin, acute at apex, abaxially densely sericeous, strongly appressed in anthesis; glands $2.3-3.5 \mathrm{~mm}$ in diameter, obovate to rotund. Petals glabrous; lateral petals with the claw $3.7-4.3 \mathrm{~mm}$ long, obtriangular and $2.2-2.5 \mathrm{~mm}$ wide at apex, the limb $7-7.5$ mm long, $8-10 \mathrm{~mm}$ wide, deeply concave, oblate to rotund, erose and eglandular at margin; posterior petal with the claw 3.5 mm long, stout ( 0.8 mm in diameter), not constricted at apex, the limb 5.5 mm long and 4.2 mm wide, rectangular, reflexed in the distal half, glandular-fimbriate with the proximal fimbriae longest. Filaments $2-2.5 \mathrm{~mm}$ long, connate in the proximal $1 / 3$; anthers $1.8-2 \mathrm{~mm}$ long, alike, reflexed, glabrous. Styles basally sericeous, $2.5-3 \mathrm{~mm}$ long, erect proximally and divergent in the distal half (but becoming strongly divergent with age), all with the stigmas much wider than high (ca. 0.6 mm wide, 0.3 mm high), dorsally obtusely apiculate at apex. Mericarp with the nut roughly ellipsoidal, $15-20 \mathrm{~mm}$ long, $10-13 \mathrm{~mm}$ wide, with several prominent parallel longitudinal veins on each side converging in a subhorizontal ridge near apex where the lateral wing would develop in other species, sericeous or appressed-tomentose, the hairs brown, persistent; lateral wings absent; dorsal wing encircling distal $1 / 2-2 / 3$ of the nut, a crest arising abruptly at style and extending over the apex and about $1 / 2-2 / 3$ down the dorsal edge, ca. 4-5 mm wide, widest near apex of nut, 15-17 mm high, somewhat revolute, sericeous; ventral areole 4.5 mm high, 3.5 mm wide, ovate.

Phenology. Flowering in January.
Distribution (Fig. 1). Known only from low-elevation forests in eastern French Guiana, near the coast; to be expected in Amapá, Brazil.

[^1]

FIG. 7. Lophopterys splendens. a. Flowering branch, $\times 0.5$. b. Enlargement of adaxial surface of lamina to show reticulum, $\times$ ca. 2.5 . c. Flower bud, $\times 2.5$. d. Flower, side view, and posterior petal, flattened, adaxial view, both $\times 2$. e. Anthers, adaxial view (left) and abaxial view (right), $\times 5$. f. Gynoecium, anterior style in center, $\times 5$, and adaxial view of tip of anterior style, $\times 10$. g. Fruit with only two mericarps developed, $\times 1$. (Based on: a-f, Oldeman B.2666; g, photograph and drawing of type.)
locality, fl, Martin s.n. (BM); Crique Simon, basse crique Courouaïe (affluent basse Approuague), Jan fl, Oldeman B. 2666 (CAY, MICH).

See the discussion of this species above under circumscription of the genus. As noted there, the lateral wings present in the samara of other species have been lost and the dorsal wing is also much reduced, to a crest only $4-5 \mathrm{~mm}$ wide. In
contrast to the reduced wings, the nut of the mericarp here is much larger than that of the samaras found in the rest of the genus; even the largest samara found in the other species has a spheroidal nut only 14 mm in diameter, much smaller than the ellipsoidal nut in L. splendens. The result is an enlarged unwinged mericarp, surely adapted for dispersal by water. Such shifts from wind-dispersal to water-dispersal have evolved repeatedly in neotropical Malpighiaceae that grow near lowland rivers, at least once in almost every wing-fruited genus. Some examples are Banisteriopsis sepium (Adr. Juss.) B. Gates and Diplopterys cabrerana (Cuatrec.) B. Gates (Gates 1982), Hiraea quapara (Aubl.) Sprague (W. Anderson 1993), Jubelina riparia Adr. Juss. in Deless. (W. Anderson 1990a), and Stigmaphyllon adenodon Adr. Juss. and S. lacunosum Adr. Juss. (C. Anderson 1997).

Of the four known collections of this species, only Hequet 388 and Oldeman B. 2666 are accompanied by data about the locality or notes on the plant. Oldeman described it as a small tree about 6 m tall, which is a surprise in a genus in which all the other species are woody vines, and Hequet described his collection as a liana. Shifts in habit from vines to small trees do occur in other genera of Malpighiaceae, e.g., Banisteriopsis and Heteropterys, and in at least one case the shift accompanied the loss of the samara's wing [Heteropterys laurifolia (L.) Adr. Juss. to H. lindeniana Adr. Juss.; W. Anderson, pers. obs.], so it may be that Lophopterys splendens is facultatively arborescent.

Lophopterys surinamensis (Kosterm.) Sandwith, Kew Bull. 1951: 37. 1951. Dolichopterys surinamensis Kosterm., Recueil Trav. Bot. Néerl. 32: 279. 1935.Type: Suriname. Upper Gran Rio, 6 Mar 1926 fr, Stahel 223 (holotype: U! [MICH negs. 3493, 3494]; isotype: K!).

Fig. 8.
Woody liana; stem hairs dark brown fading to stramineous or gray. Lamina of larger leaves $16-19.7 \mathrm{~cm}$ long, $8-10 \mathrm{~cm}$ wide, obovate, broadly truncate to subcordate and sometimes unequal at base, nearly plane at margin, very broadly rounded and deeply emarginate at apex, eglandular, glabrate above at maturity except for sparse pubescence persistent along midrib, densely and persistently sericeous below with the rather loose hairs giving the dried leaf a bronze sheen, the $8-11$ pairs of lateral veins prominent below, interconnected by prominulous parallel secondary veins, the intricate reticulum prominulous on both sides; petiole $15-20 \mathrm{~mm}$ long, persistently sericeous, bearing $1-3$ pairs of sunken glands in the distal $2 / 3$ on sides near adaxial edges; stipules not found. Inflorescence persistently subvelutinous with the hairs dark brown, ca. 30 cm long, terminal, a panicle with the pseudoracemes $17-23 \mathrm{~cm}$ long and containing ca. 25-50 flowers, the axis $2-4 \mathrm{~mm}$ in diameter; bracts and bracteoles abaxially loosely sericeous, mostly deciduous in fruit, triangular, appressed; bracts $2-3 \mathrm{~mm}$ long, $1.2-2 \mathrm{~mm}$ wide; peduncle $0.4-1 \mathrm{~mm}$ long in fruit; bracteoles $1-1.5 \mathrm{~mm}$ long, $0.6-1 \mathrm{~mm}$ wide; pedicel $6.5-7.6 \mathrm{~mm}$ long, $2-2.5$ mm in diameter at apex in fruit, velutinous. Anterior sepal broadly triangular, 2 mm long and 2.5 mm wide in fruit, abaxially appressed-tomentose, appressed; lateral sepals not exceeding the glands in fruit; glands $3-4 \mathrm{~mm}$ long and wide, transversely elliptical to circular. Petals, androecium, and gynoecium not seen. Samara with the nut spheroidal, $10-14 \mathrm{~mm}$ in diameter, smooth on sides and between wings, appressed-tomentose, the hairs brown to stramineous and persistent or patchily deciduous; lateral wings $48-60 \mathrm{~mm}$ long, $6.5-11 \mathrm{~mm}$ wide, very narrowly elliptical and abruptly narrowed distally to a rounded or obtuse apex, loosely sericeous to glabrate, the hairs stramineous; dorsal wing half-encircling


FIG. 8. Lophopterys surinamensis. a. Leaf, adaxial view, $\times 0.5$, with enlargement of surface of lamina to show reticulum, $\times$ ca. 5. b. Fruit with only one samara developed, lateral view (above) and abaxial view (below), both $\times 0.8$. (Based on the holotype, Stahel 223.)
the nut, trapezoidal-flabellate, $12-15 \mathrm{~mm}$ wide, $20-25 \mathrm{~mm}$ high, entire or sinuate, loosely sericeous to glabrate; ventral areole $6-7.5 \mathrm{~mm}$ high and wide, ovate to subcircular; inner face of seed locule appressed-tomentose.

Phenology. Fruiting in early March.
Distribution (Fig. 1). Known only from the type, from central Suriname.
The type of Lophopterys surinamensis bore only submature fruits. Consequently, almost nothing is known about the petals, stamens, and styles in this species. In order to place it in the key to flowering specimens we have had to assume that its anthers are glabrous.

In its inflorescence and fruit this species resembles L. euryptera of Guyana and adjacent Venezuela, but it is immediately distinguished by its much smaller leaves with shorter petioles, which resemble those of L. splendens of French Guiana. The three species seem to form a complex of the Guianas.

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[^0]:    1. Anther locules pilose with obvious spreading hairs.
    2. Peduncle $0.5-2.5(-3) \mathrm{mm}$ long; pedicel $2-4 \mathrm{~mm}$ long; hairs brown or dark brown throughout the inflorescence.
    L. floribunda.
    3. Peduncle (2-) $2.5-4 \mathrm{~mm}$ long, with at least some peduncles in every inflorescence 2.5 mm long or longer; pedicel $3.3-5(-6) \mathrm{mm}$ long; hairs golden-brown or golden on ultimate axes of inflorescence, especially peduncles and pedicels.
    L. occidentalis.
[^1]:    Additional Specimens Examined. French Guiana. Layon Montagne Prise d'Eau, bassin de l'Approuague, $^{2} 04^{\circ} 28^{\prime} \mathrm{N}, 52^{\circ} 02^{\prime} \mathrm{W}$, forêt de pente de basse altitude, Jul ster, Hequet 388 (U); without

